

VICARIANCE BIOGEOGRAPHY IN MESOAMERICA

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ABSTRACT

This paper sets out to achieve three objectives. A brief introduction gives the present position of cladistic biogeography. Secondly, the most recent developments in cladistic biogeography for resolving complex and apparently incongruent species cladograms are presented. Thirdly, the methods as applied to the interrelationships of endemic areas in Mesoamerica with particular respect to the data of Rosen (1975, 1978, 1979) on poeciliid fishes is given.

INTRODUCTION

The analysis of spatial and temporal distribution of life on earth is the principal concern of historical biogeographers. Although many people would agree with this statement, there is still considerable disagreement amongst biogeographers about which methods should be used for the study of distribution and how distributions contribute information about the interrelationships and origins of areas. Distribution patterns can be analyzed in at least three different ways: first, we can compare the number of species or groups of species in different regions and say how many are common to each, thus getting a measure of overall similarity. Second, we can note the species and genera within one region and compare them with the species and genera of another and speculate where and how they might have arrived there. Third, we can make a comparison of the cladistic relations of various groups of organisms occurring in a group of areas of endemism to develop hypotheses on the historical connections of biotas in space and time—the pursuit originally identified by Nelson (1975) and Nelson and Rosen (1981) as vicariance biogeography and called cladistic biogeography by Parenti (1981).

Historical biogeography, by any method, is an integration of taxonomy and historical earth science. A comparison of taxonomies in different groups is the basis for determining biogeographic patterns. Historical biogeography is thus an integral part of systematics and a slave to its theoretical foundations. Invariably, changes in historical biogeographic theory follow changes in taxonomic theory. There have been numerous developments in the post-war period and today major divisions exist between the practitioners of cladistics, evolutionary systematics, and phenetics with parallel divisions in historical biogeography between the methods of cladistic biogeography (e.g., Nelson & Platnick, 1981), dispersalism (Darlington, 1965), and area phenetics (e.g., Holloway & Jardine 1968). I would like to concentrate my efforts on the most recent and most thorough developments in systematics and biogeography—cladistics and vicariance. Most of the ideas presented here do not claim my originality, but are the ideas of three zoologists from the American Museum of Natural History—D. E. Rosen, G. Nelson, and N. I. Platnick—and one botanist, L. Croizat, now resident in Vene-

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zuela, who have all done so much to put historical biogeography into a scientific framework.

In the view of Patterson (1981), analytical systematics has been developed by three groups of workers: those workers who have adopted numerical methods for explicit phylogeny construction (e.g., Kluge & Farris, 1969; Farris et al., 1970; Farris, 1970); those taxonomists like myself influenced originally by Hennig's phylogenetic systematics (see Hennig, 1965, 1966); and those biochemists who have independently developed methods of reconstructing phylogenies from molecular data (e.g., Fitch & Margoliash, 1967; Moore et al., 1973; Fitch, 1977). These methods all have various features in common which distinguish them from narrative procedures. They all have taxa or empirical units as terminal branches in the relationship diagrams and the method for producing the diagrams is to interpret the most economical or most parsimonious distribution of homologies (i.e., characters, components, synapomorphies) (Patterson, 1981). As the basic method for producing the diagrams was developed independently in the three different fields, its superiority over narrative methods lies in its simplicity and its accessibility to criticism. By insisting on one property—homology, and only one criterion—parsimony, cladistics is as scientific a method as anyone can use in systematics. Narrative systematics on the other hand allows any explanation and thus immunizes itself against criticism.

Patterson (1981) when reviewing the recent history of efforts to clarify the basis of historical biogeography concludes that cladistic biogeography is a development within cladistics. Analytical or vicariance biogeography is the pursuit of a method which encompasses a code comparable to cladistics. By gradually shedding *a priori* assumptions such as dispersal, extinction, allopatry, and sympatry it has increased our chances of understanding pattern and area interrelationships without circular evolutionary reasoning. In other words, if we are to understand the products of evolution we cannot use the existing principles to interpret patterns. By changing the word homologies to sister groups cladistic biogeography interprets the geographical distribution of sister groups parsimoniously. Different patterns when added together generate general hypotheses of area interrelationships. Thus, by using the two criteria of monophyletic sister groups and parsimony, cladistic biogeography is as scientific a method as anyone can use in historical biogeography.

BIOGEOGRAPHIC PATTERNS IN MESOAMERICA

Both 'centers of origin' and 'vicariance' hypotheses are biogeographical statements that presuppose that areas of endemism are interrelated and that these patterns are identifiable. What does it mean though to say that two areas of endemism are related to one another? We could pick on any two areas of the world and pick on any reason to say that they are biogeographically related to one another. For example, consider the southeastern states of North America and the tropical parts of Central America (Fig. 1). The fact that they have many groups of organisms in common means that they are related. But, do numbers really mean anything? We could equally pick on one endemic species from each area and say that these two are related, if only by saying that they belong to the

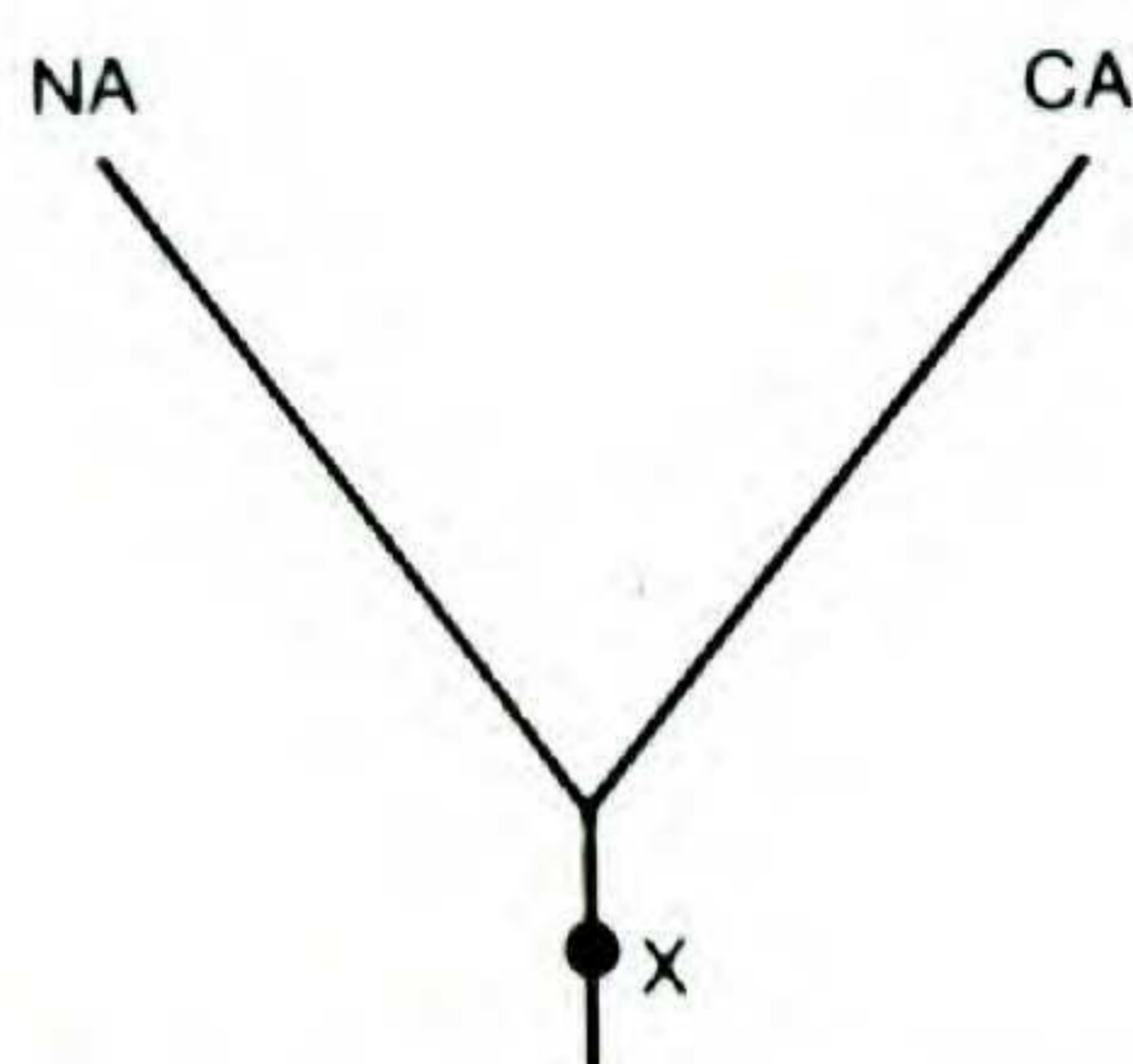


FIGURE 1. Branching diagram depicting a 2-area statement. The areas of North America and Central America are related to one another by the shared component(s) x.

same family. It is meaningless, however, to say that two areas such as North and Central America are related without some reference point to say by how much. We need, just as in statements of cladistic relationships, a minimum of three areas to express the interrelationships of two.

Consider the following example. By examining the distribution pattern of the *Acer saccharum* group (Fig. 2) there are three obvious disjunct areas—the southeastern United States (1), eastern Mexico (2), and northern Central America (3). For three such areas there are three possible ways of expressing a resolved, or fully informative relationship (Fig. 3 a, b, c).

Before it is worth answering the question of which of the three patterns is correct, it is worth answering the question does the *Acer saccharum* pattern belong to a more general pattern indicated by the three areas 1, 2 and 3? This is exactly the type of question that Croizat (1958, 1962) asked of his panbiogeographic method, and also Rosen (1975, 1978) in his studies of Caribbean biogeography. Rosen gathered a whole range of distributional data for various groups and plotted them on maps. Major disjunctions between different areas were then connected by lines or tracks. A search was then made to establish replicated or generalized tracks which indicated a common cause for the pattern. Rosen (1975) performed this type of analysis for twenty-one groups of fishes and amphibians and established that there were five major distribution tracks for Mesoamerican and Caribbean regions (Fig. 4); a North American-Caribbean track, an eastern Pacific-Caribbean track, an eastern Atlantic-western Atlantic track, and an eastern Pacific-eastern Atlantic track. The two terrestrial tracks are illustrated in Fig. 4.

Rosen (1978) showed that by examining the detailed distribution patterns of particular taxonomic groups and phylogenetic relationships, a resolved pattern of area interrelationships could be obtained. By looking at the distribution of one hundred and fourteen fish species occurring in ten river systems from the Rio Grande to the Rio Papaloapan, Rosen showed a higher probability that the areas 2 and 3 (Fig. 2) were more closely related to one another because the nominal sister group relations were congruent in the expression of such a pattern. Of the one hundred and fourteen taxa, thirty-six are endemic to the Rio Grande, none is endemic in the next two rivers south, fourteen are endemic to the Rio Panuco Basin, and thirty-five occur only in the rivers south of the Rio Panuco. Of the thirty-six in the Rio Grande, some are the same as, and others are most closely related to, species of the southeastern United States (thus showing that the Rio Grande is part of a much larger region of endemism). Of the thirty-five

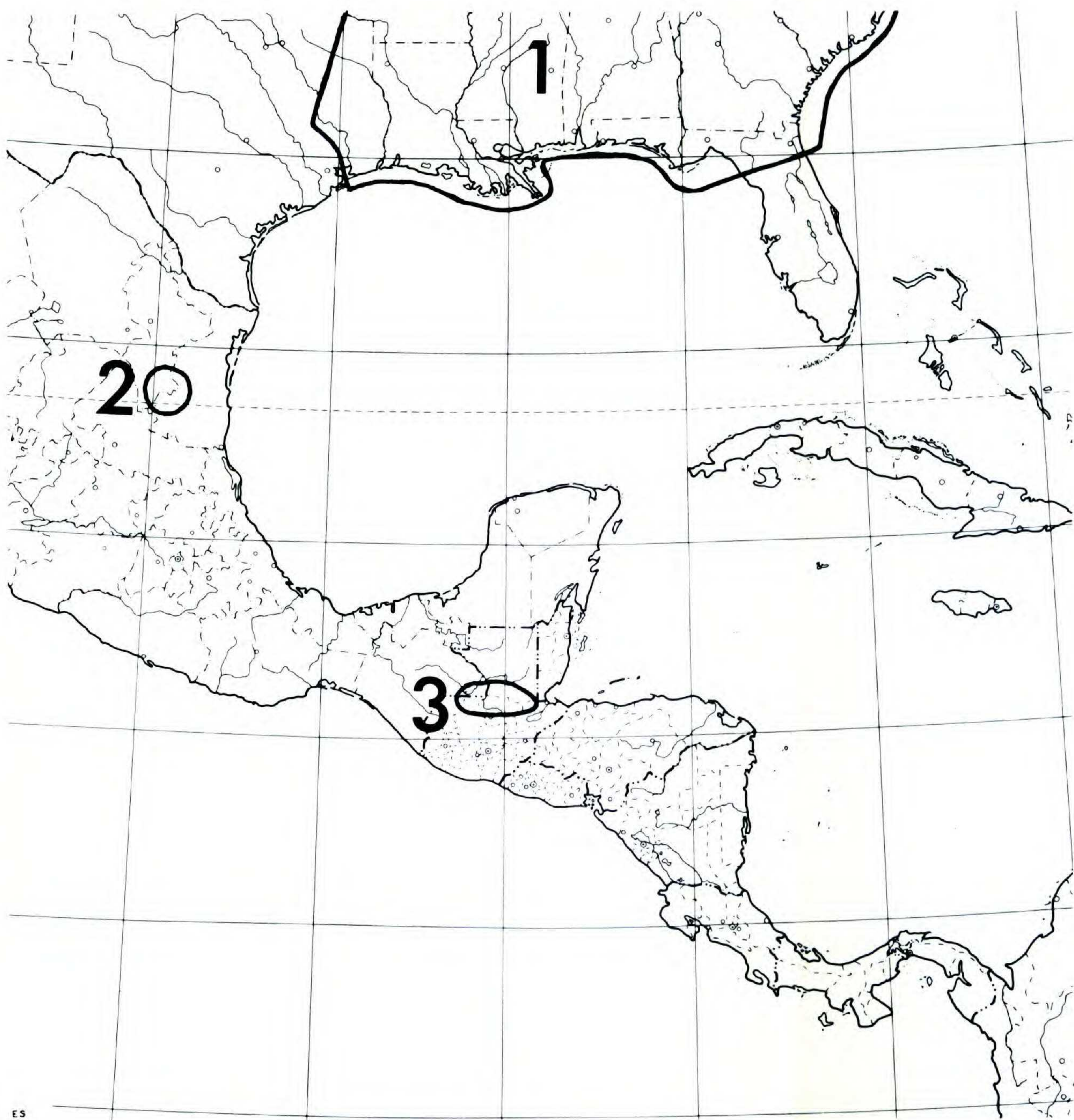


FIGURE 2. The occurrence of *Acer saccharum* group in middle and North America.

taxa in the six rivers south of the Rio Panuco, some are the same as, and others are most closely related to, species in the remainder of southeastern Mexico and northern Central America. The interrelationships of the three disjunct areas are thus defined and the patterns suggest that areas 2 and 3 are more closely related to one another than they are to area 1. For the *Acer saccharum* group the taxonomy is sufficient to resolve that areas 2 and 3 are more closely related to one another than area 1.

The question one might ask now is: what are the implications of this type of statement? The answer would be that an initial vicariance event is postulated as having occurred somewhere between the Rio Grande and the Rio Panuco Basin followed by a second, later, vicariance event dividing the Rio Panuco Basin and southern Mexico with Central America. At this level of resolution three-area

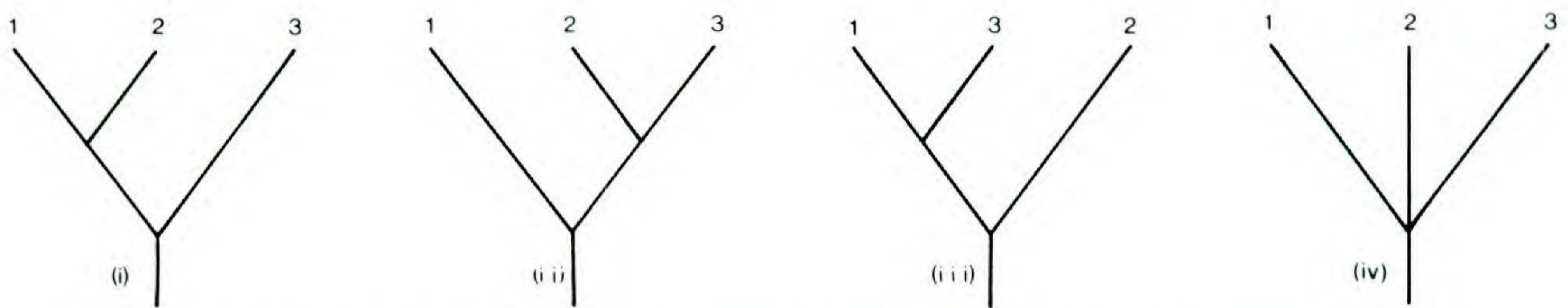


FIGURE 3. Branching diagrams to show the full range of cladistic relations for 3 areas.

cladograms give only simple answers. Despite the effort involved for producing three-area cladograms, several two-step paleogeographic events can be correlated with the cladograms to give two such obvious disjunctions. To get a much more significant result it is necessary to look at the detailed relationships of groups which occupy all or most of the identifiable endemic areas.

The detailed distribution patterns of many groups with three or more taxa are known for Mesoamerica, but detailed phylogenetic hypotheses for plant groups can be counted on one hand. Analytical biogeography is extremely demanding, ideally requiring many phylogenetic studies of widely different, randomly selected groups occupying similar areas (see Humphries, 1981). Recently published botanical cladograms include those of Judd (1981), Bolick (1981), and Sanders (1981), but the groups on which they worked do not occur in identical endemic areas and so do not make a detailed analysis possible. Rosen's (1975, 1978, 1979) work on the poeciliid fish genera *Heterandria* and *Xiphophorus* can serve as a more detailed study of groups occupying several areas and demonstrates the latest developments in analytical biogeography. Although these studies may be familiar to the botanical community, particularly through the paper and book of Wiley

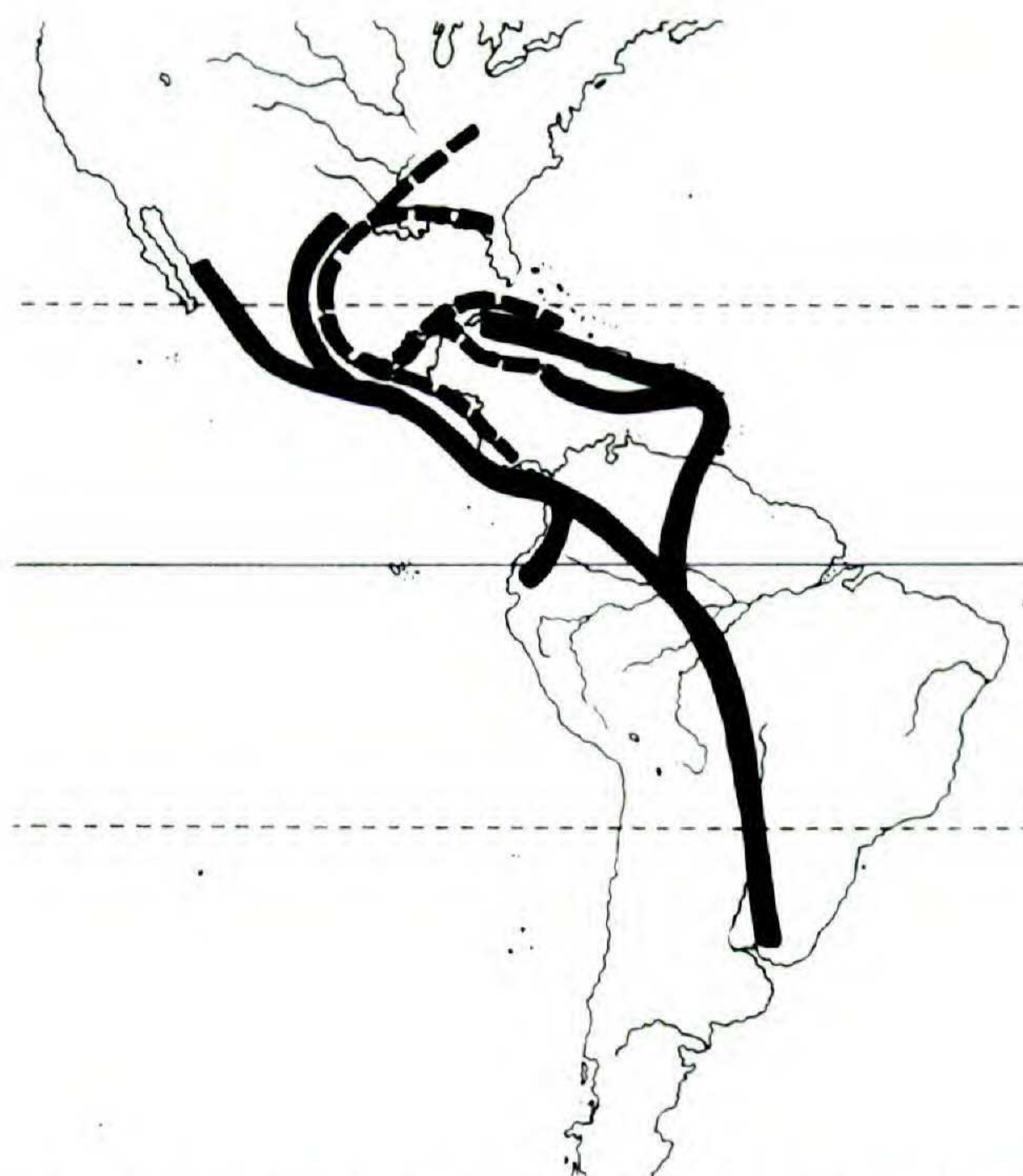


FIGURE 4. Summary of transcontinental generalized tracks. Overlapping of North and South American tracks enclosing the Caribbean sea (after Rosen, 1975, Fig. 6C).

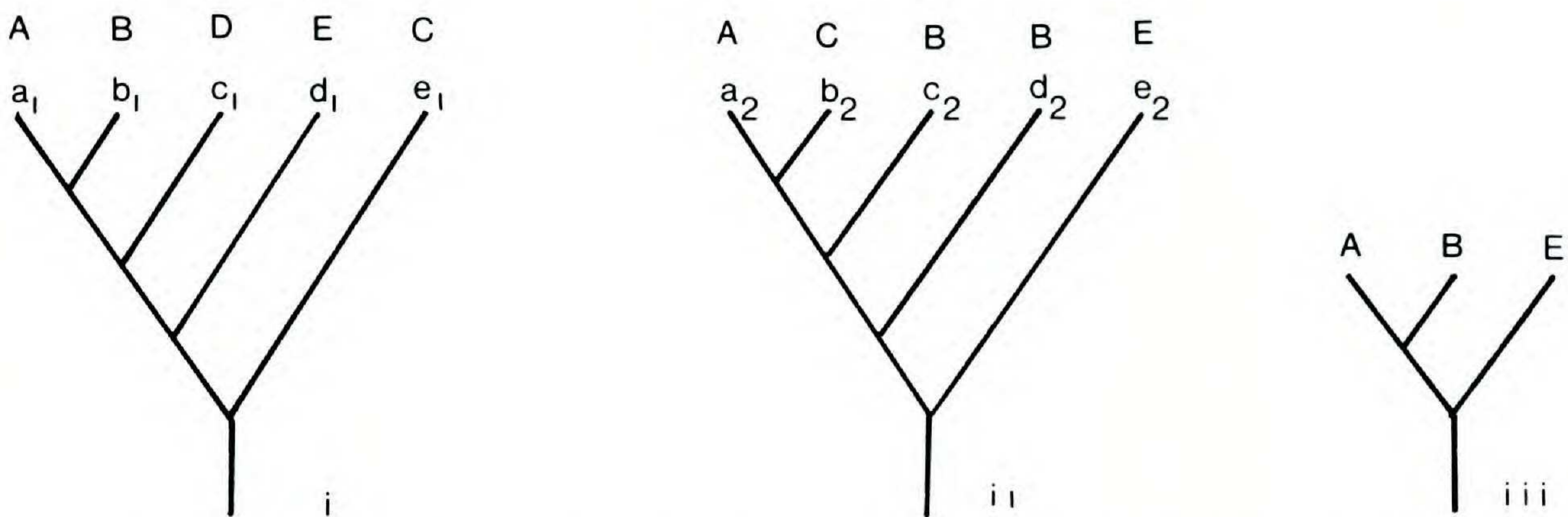


FIGURE 5. i, ii. A comparison of two area cladograms. iii. Reduced consensus cladogram showing common components to cladograms i and ii.

(1980, 1981), they have been undertaken under restrictive assumptions (Platnick, 1981) and are thus worthy of another consideration, since they still remain the only fully worked examples for the areas of our concern.

TRANSFORMING DATA—A THEORETICAL ASIDE ON COMBINING CLADOGRAMS

Before considering the explicit examples of *Heterandria* and *Xiphophorus*, it is necessary to consider the notion of compatibility or congruence between cladograms in more detail. To search for congruence between different cladograms occupying similar areas, the taxa are substituted by area notations to give area cladograms (Rosen, 1975, 1978, 1979). If, when compared, several phylogenies match one another, we can, as seen earlier, hypothesize that congruence is due to a common history. However the success with which we find congruence is reduced by the number of unique patterns affecting the distribution and origin of each group of organisms. In other words, when several groups are compared and show incongruent patterns they might still have had similar evolutionary histories. Apparent incongruences might be due to a number of factors giving incongruent and unresolved patterns in the original taxonomy, all of which can give errors in interpretation of their meaning. To overcome these problems we cannot resort to interpretations of evolutionary process, but we can use only the logic of cladograms and develop ways of adding cladograms together to give us general area statements (see Nelson & Platnick, 1981). So far two main methods for dealing with incongruences have been described, Rosen's method of reduced area cladograms and Nelson and Platnick's method of component analysis, although Mickovitch's transformation series analysis might be yet another technique.

1. ROSEN'S METHOD OF REDUCED AREA CLADOGRAMS

The technique of reduced area cladograms was put into practice by Rosen (1978). It is designed to find a common pattern for the areas of two or more different groups of taxa by eliminating unique or incongruent elements from the individual groups. Consider the two cladograms in Fig. 5 i, ii. In the first group the five taxa a, b, c, d, e occur in five areas A, B, C, D, and E. In the second group the five taxa a, b, c, d, and e occur in four areas A, B, C, and E. Area D

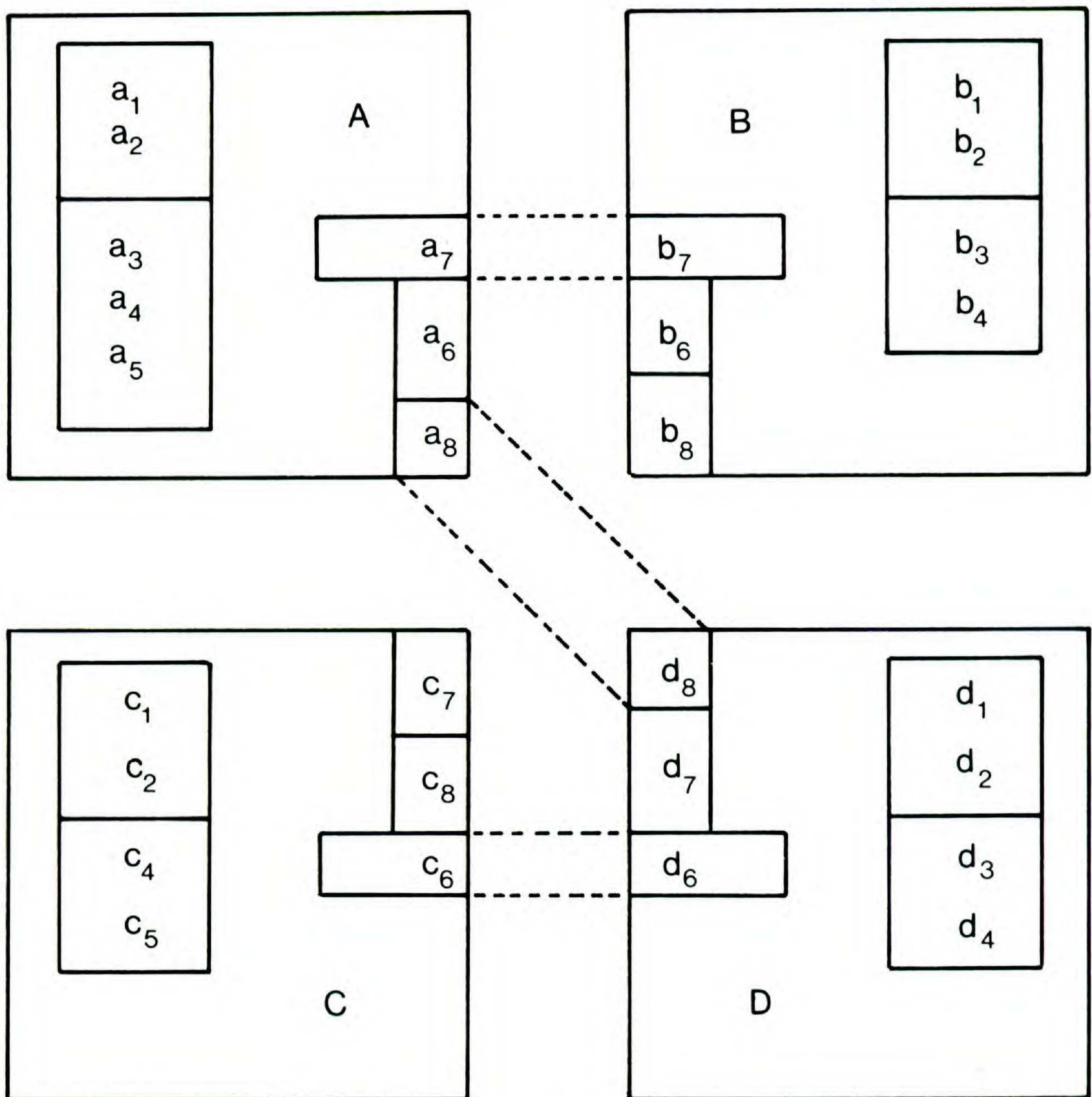


FIGURE 6. Hypothetical map for four areas ABCD, and the hypothetical distribution of eight taxonomic groups, $a_1 b_1 c_1 d_1$, $a_2 b_2 c_2 d_2$, $a_3 b_3 c_3 d_3$, $a_4 c_4 d_4$, $a_5 b_5 c_5$, $a_6 b_6 c_6 d_6$, $a_7 c_7 d_7$, $a_8 b_8 c_8$.

is unique to the first cladogram and so is considered to be uninformative. Area C occurs in different positions on the two cladograms and is thus considered to be incongruent. Since area B is only a single area in geographical terms its appearances for both taxa, c and d, in the second cladogram can be reduced to a single terminal statement in the consensus cladogram (Fig. 5 iii). The consensus cladogram produces a statement of those areas, A, B, and E, which share a common history.

2. NELSON'S AND PLATNICK'S METHOD—COMPONENT ANALYSIS

For the purposes of discussion consider four hypothetical areas ABCD and the hypothetical distribution of eight different hypothetical groups of taxa, labelled for the sake of convenience 1–8 (Fig. 6, Table 1). The first two groups of taxa, numbered abcd 1 and 2, each have one endemic in each of the four areas of

TABLE 1. The distribution of eight groups of taxa in four areas—see Fig. 6 and text for explanation.

A	B	C	D	Areas
a ₁	b ₁	c ₁	d ₁	} one endemic in each area
a ₂	b ₂	c ₂	d ₂	
a ₃	b ₃	*	d ₃	} one extinction in each area
a ₄	*	c ₄	d ₄	
a ₅	b ₅	c ₅	*	
a ₆	b ₆		(cd ₆)	} one widespread taxon in two areas
(ab ₇)		c ₇	d ₇	
ad ₈	b ₈	c ₈	ad ₈	

our concern. The second group of taxa, numbered abcd 3, 4, and 5, and have less than ideal distributions since they have one missing taxon from each of the areas of our concern. The third group of taxa numbered also have less than ideal distributions since each group has three taxa with a widespread species occurring in two of the four areas.

In the first example, involving the first two groups of taxa, the geological hypothesis (Fig. 7) indicates that the areas AB are more closely related to one another than they are to either C or D and at some relatively earlier point in time the areas ABC were more closely related to one another than to the fourth area D. The two biological cladograms are perfect in the sense that they have endemic taxa in each of the four areas and the cladograms indicate complete resolution of their relationships. They show complete congruence with the geological cladogram and yield only the same area components as indicated in Fig. 7 i–iii by the numbered black dots next to the branch points.

The second example shows the problem of how to obtain information about the interrelationships of areas in the absence of geological cladograms and with imperfect cladograms, since each has a different endemic missing from one of the areas (Fig. 8 i–iii). Looking at all three cladograms individually there is a range of different area components (see Fig. 8 i–iii, 0–5). Thus Fig. 8 i has two components, labelled 0 and 3, Fig. 8 ii has two components labelled 4 and 5 and Fig. 8 iii shows two components labelled 2 and 3.

Since each cladogram has only three terms (i.e., terminal taxa), they have only two rather than the requisite three components to identify the relationships of four areas. In other words they each lack the fourth area, ABCD, component 1. Also, if we assume that the relationships of the three groups of organisms are the result of similar historical causes then two of the apparent components in the array given by the the three cladograms (Fig. 8 i–iii) must be false since only two can be true to give a fully resolved cladogram of four areas. As each cladogram has three of the four terms required, the missing term can be added. As shown in Fig. 9 the missing term can be added in one of five different places. Since for any one cladogram we do not know where to add the missing term, this means that we have five possible results for the interrelationships of areas. For example, consider the cladogram in Fig. 8 i. By adding the missing C term the five fully restored cladograms can be seen in Fig. 9 i–v. Similarly, for the cladogram shown in Fig. 8 ii the missing B term can be added as shown in Fig. 9 i, iii, iv, vii, ix

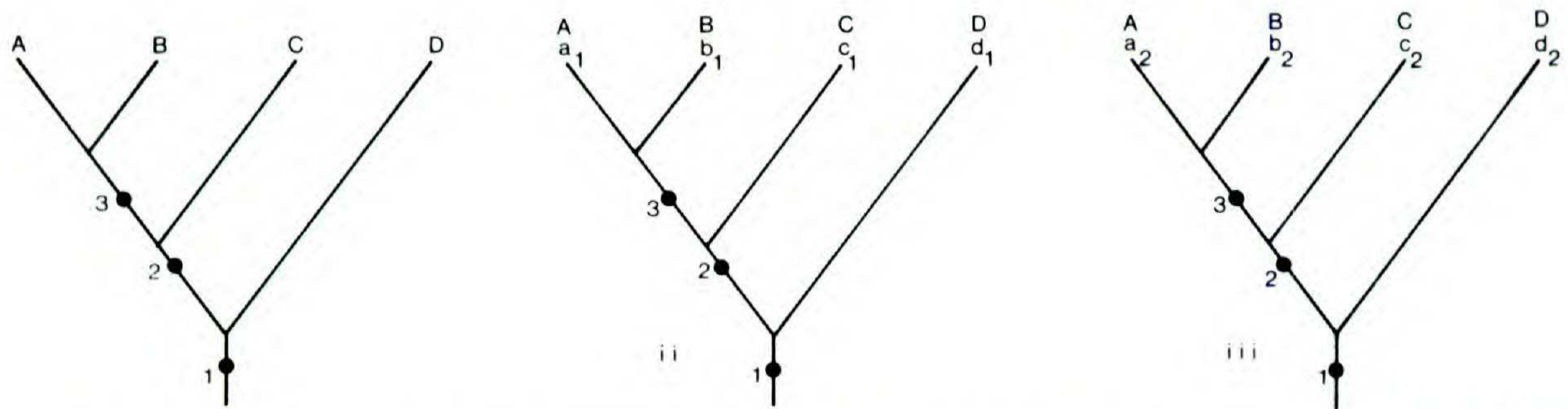


FIGURE 7. Hypothetical area cladograms. (i) cladogram for four areas ABCD defined by three components 1, 2, and 3 (ii) + (iii) cladogram for two groups of four taxa $a_1 b_1 c_1 d_1$ and $a_2 b_2 c_2 d_2$ and the areas in which they occur also specified by 3 components 1, 2, and 3 (see text for explanation).

and similarly for the cladogram shown in Fig. 8 iii the missing D term can be added as shown in Fig. 9 i, ii, v, vi, viii. In other words, of the fifteen possible cladograms, eight of them, representing more than 50% of the total, are reiterated. Four of the complete cladograms (Fig. 9 vi–ix) account for only one of the partial cladograms. Similarly, four of them account for two of the partial cladograms (Fig. 9 ii–v) and only one (Fig. 9 i) actually accounts for all three of the partial cladograms. Thus, if the patterns of the three partial 3-taxon cladograms are due to common history, then the only information in them about the interrelationships of the four areas is the cladogram in Fig. 9 i, which must be the correct one. This cladogram identifies the components 1, 2, and 3 as real and the components 0, 4, and 5 as misleading due to missing information. But assuming all of the original components as real is a problem since when they are added together they give a

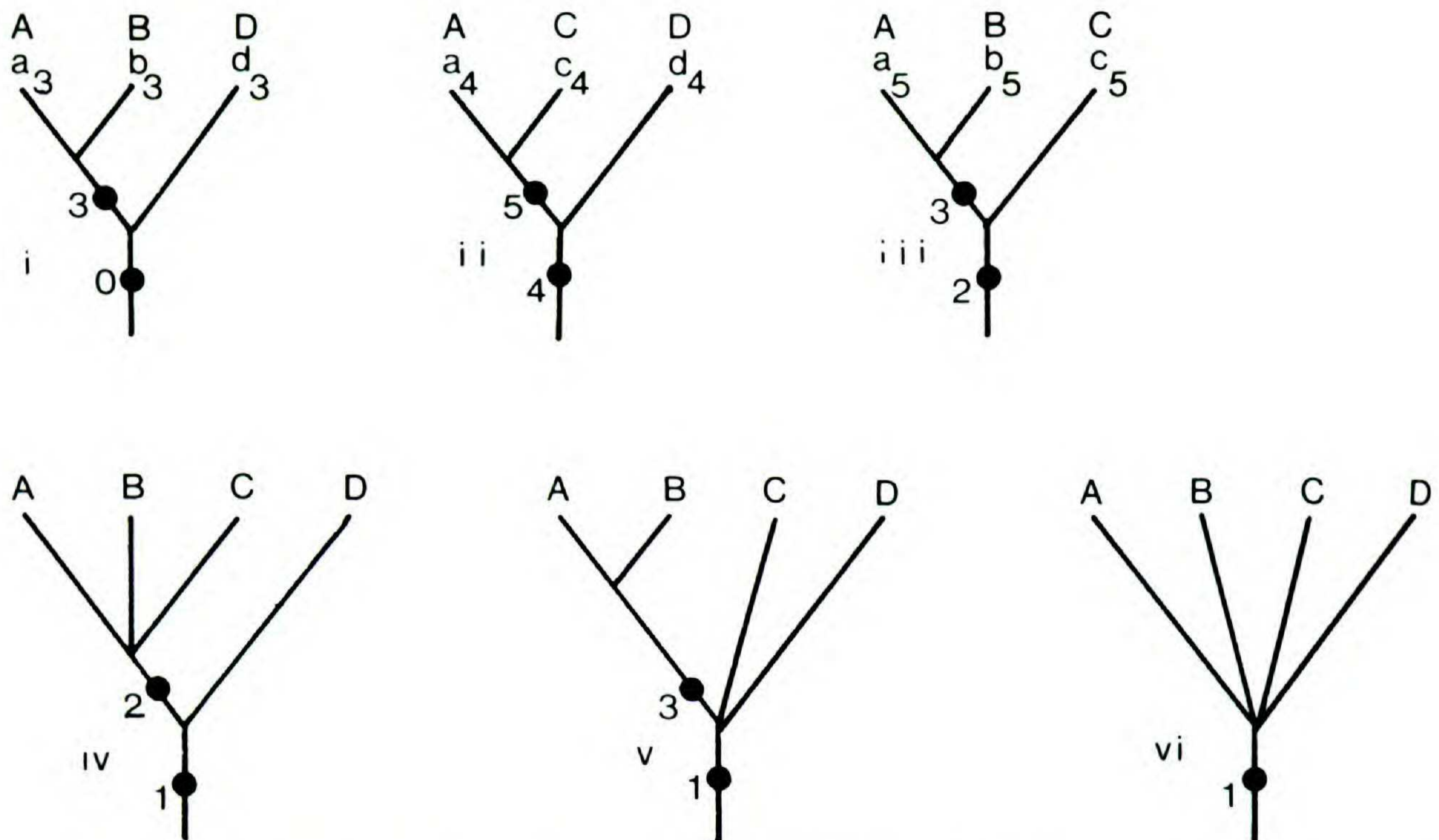


FIGURE 8. Hypothetical area cladograms for three groups of three taxa, $a_3 b_3 d_3$, $a_4 c_4 d_4$, $a_5 b_5 c_5$, (i, ii, & iii) occurring in four areas; (iv), (v), and (vi) generalized area cladograms obtained by adding together cladograms i + ii, ii + iii, and i + ii + iii respectively (see text for explanation).

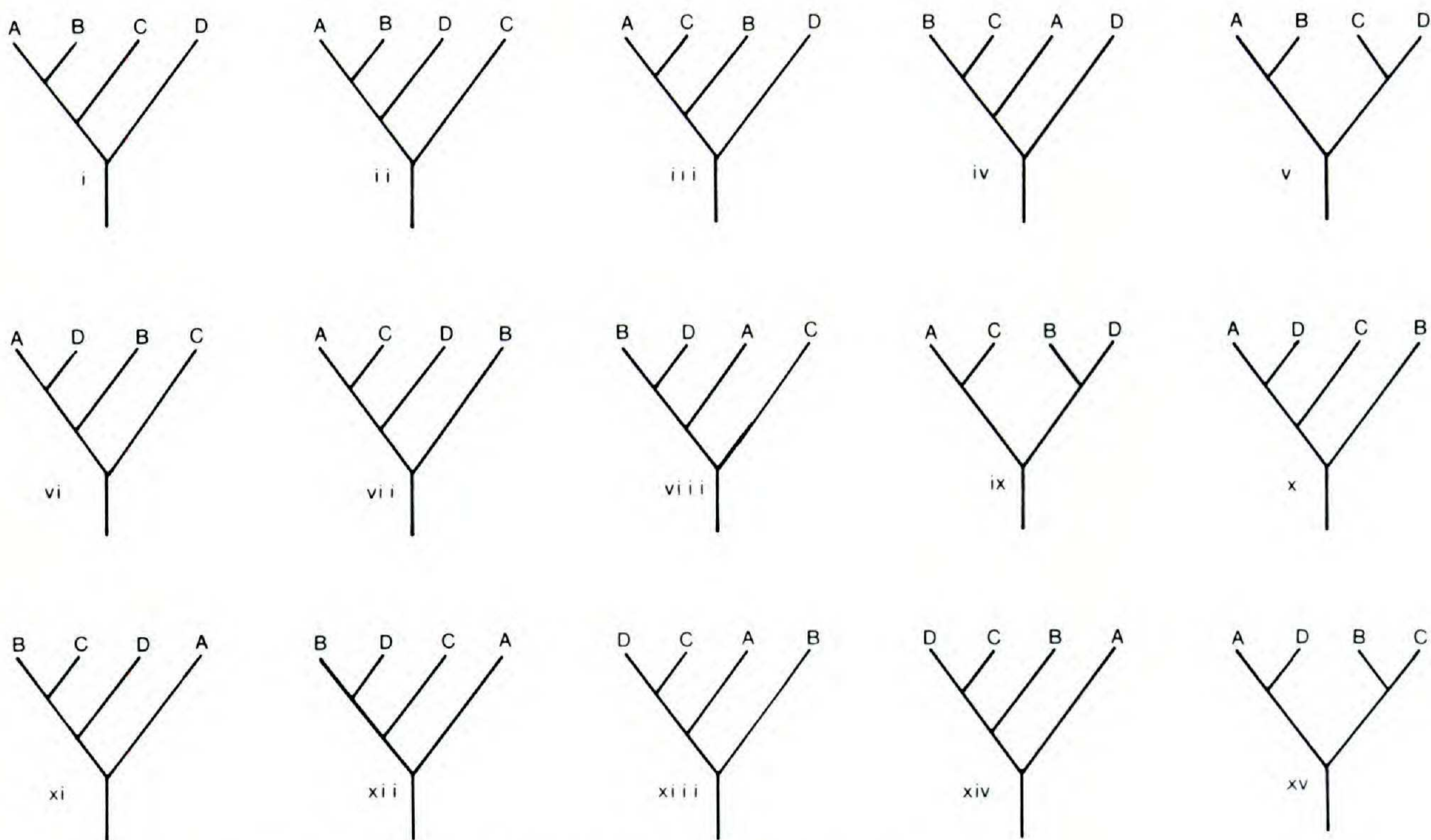


FIGURE 9. The fifteen possible resolved cladograms for four areas.

totally uninformative answer. By adding the cladograms in Fig. 8 i and ii together the ABCD component 1 is recovered but there is no way of resolving the AB and AC components, 3 and 5, and thus the ABC component must be left as an unresolved trichotomy (Fig. 8 iv). Similarly, by adding the cladograms in Fig. 8 i and iii together, the AB component 3 and the ABCD component 1 are both recovered but the incongruency for the 0 and 2 components leaves the AB, C, and D areas as an unresolved basal trichotomy (Fig. 8 ii). When all three of the partial cladograms are added together a totally uninformative result is obtained except for the recovery of component 1 (Fig. 8 vi).

In the third group of taxa the cladograms are characterized by each having species in all four areas but one in each of the three cladograms has one widespread species occurring in two of the areas (Figs. 10 i, ii; 11 i, ii; 12 i, ii). A comparison of the area cladograms indicates that each is less than fully informative since the widespread species give effectively unresolved area interrelationships. As was seen to some extent in the second example (Figs. 8 and 9), missing endemics can be considered under two different assumptions. Under the first assumption all of the components can be considered as informative, but under the second we can allow for missing information and apply the full cladistic logic by admitting that some of the components are false. The theoretical ramifications of assumptions one and two have been discussed at length by Nelson and Platnick (1981).

Under assumption one whatever is true of a widespread taxon (see taxon cd6 in Fig. 10 i) in one part of its range (area C, Fig. 10 ii) must also be true of the taxon in other parts of its range (area D, Fig. 10 ii). However, under assumption two whatever is true of the widespread taxon in one part of its range need not also be true of the taxon elsewhere. The implications are that under assumption

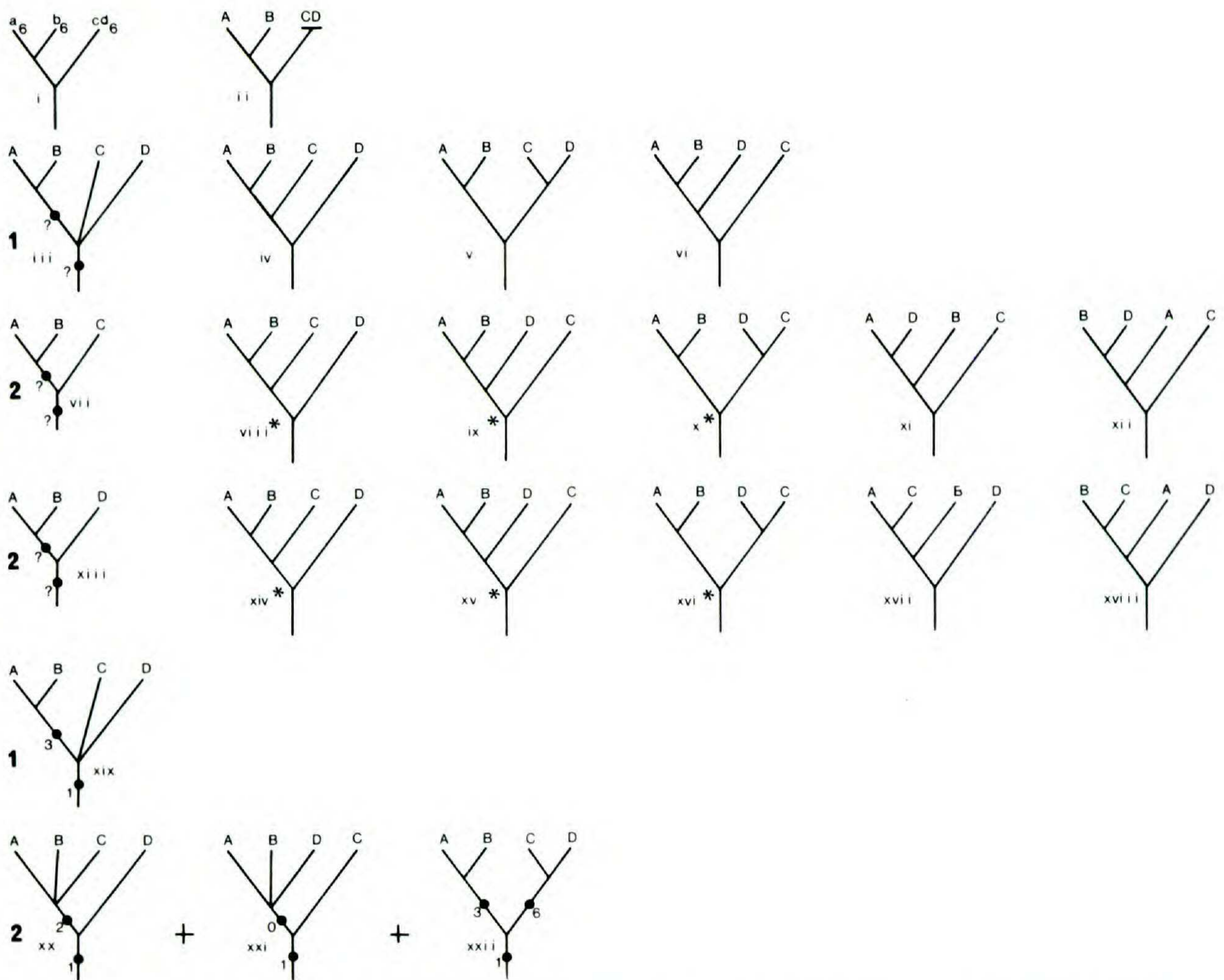


FIGURE 10. Component analysis for three taxa a_6 b_6 cd_6 (i) expressing a mixture of endemic, i.e., 1 and 2 in A and B, and widespread distributions 3 in CD (ii); (iii–vi) component analysis under assumption 1; (vii–xviii) component analysis under assumption 2; (xix) summary components under assumption 1; (xx–xxii) summary components under assumption 2. See text for explanation.

one the taxon occupying area CD will never be split into separate taxa. More precisely, if species b_6 in area B and species a_6 in area A are more closely related to each other than to species cd_6 in area C then species b_6 and a_6 are also more closely related to one another than they are to species cd_6 in area D. Under this assumption the area cladogram (Fig. 10 iii) yields a single within-group component (3 in Fig. 10 xix). Such a partially resolved cladogram would, under further analysis, allow for only three fully dichotomous cladograms (Fig. 10 iv–vi). Under assumption two the CD occurrences of taxon cd_6 might at some time be divided into two separate entities, such that whatever is true of one occurrence might not be true of another. Using the same example, if species a_6 in area A and species b_6 in area B are more closely related between themselves than to species cd_6 , the relationship might only be true for species cd_6 in area C, or, for species cd_6 in area D, but not for both. Under this assumption the area cladogram yields two possibilities for component analysis (Fig. 10 vii, xiii) but each possibility includes only three of the four areas under consideration. The two components ABC and ABD each allow for five different, fully dichotomous cladograms when

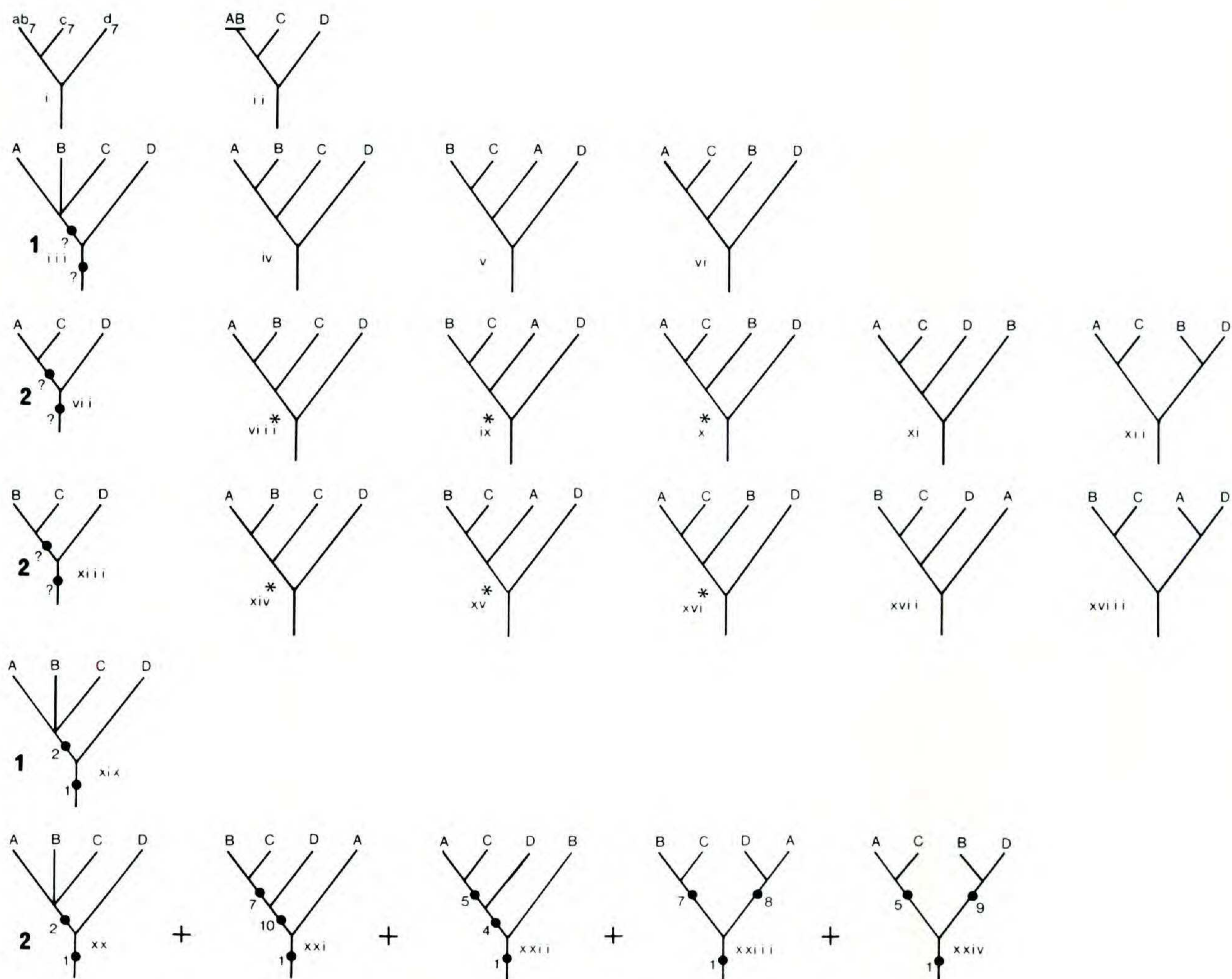


FIGURE 11. Component analysis for three taxa $ab_7 c_7 d_7$ (i) expressing a mixture of endemic, i.e., c_7 and d_7 in C and D, and widespread distributions ab_7 in AB (ii); (iii–vi) component analysis under assumption 1; (vii–xviii) component analysis under assumption 2; (xix) summary of components under assumption 1; (xx–xxiv) summary of components analyzed under assumption 2. See text for details.

the missing D and C terms are added (Fig. 10 viii–xii, xiv–xviii). A comparison of the two rows of cladograms shows that three in each are repeated (as shown by the asterisks) giving a total of seven different cladograms for the two component analyses. These results differ from assumption one by resolving four components within the ABCD group but there is conflict between components 0 and 2 (Fig. 10 xx–xxii).

Similar analyses have been carried out on two other species cladograms (Figs. 11, 12) but with the widespread species in different positions on the cladogram. Under assumption one there are three possible cladograms which, when combined together, yield two components within each group (Figs. 11; 12 iii–vi; xix, components 1 and 0). Under assumption two (Figs. 11; 12 vii–xviii) there are again seven possible different cladograms for each analysis. The summary cladograms (Figs. 11; 12 xx–xxiv) yield five different possibilities.

Combining the different area cladograms to give single general area cladograms (see Figs. 13, 14) is equivalent to combining together the implied summary cladograms of the component analyses which give the most likely solutions. For

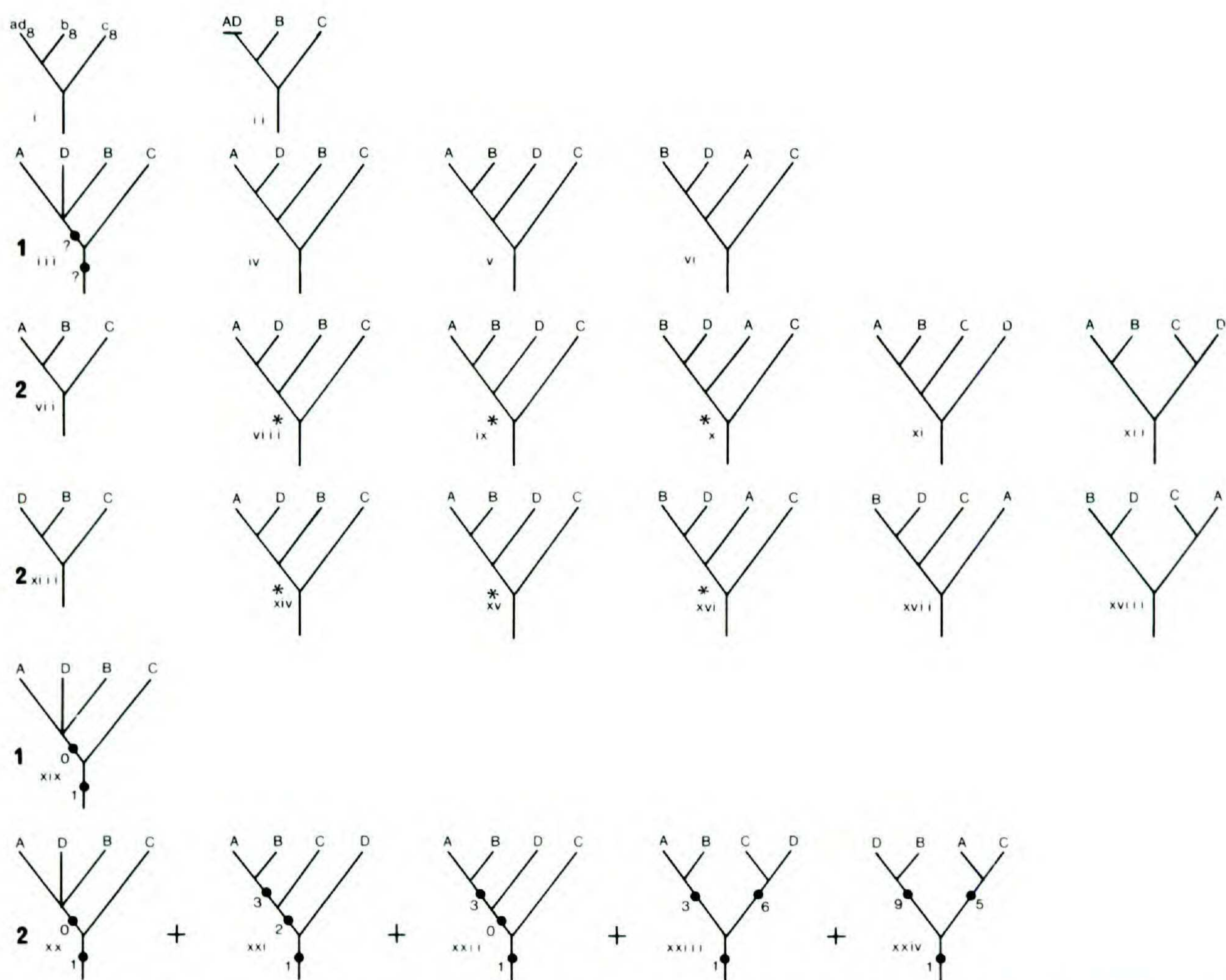


FIGURE 12. Component analysis for three taxa $ad_8 b_8 c_8$ (i) expressing a mixture of endemic and widespread distributions (ii); (iii–vi) component analysis under assumption 1; (vii–xviii) component analysis under assumption 2; (xix) summary of components analyzed under assumption 1; (xx–xxiv) summary of components analyzed under assumption 2. See text for details.

example, suppose we had the two area cladograms for the two species groups 6 and 8 (Figs. 10 and 12 i, ii). Under assumption one (Fig. 13 iii–v) combining the two cladograms would give two conflicting components, 0 and 3, and an uninformative consensus cladogram. Under assumption two there are several possibilities of which just two are shown (Fig. 13 vi–xi). For example take the implied summary cladogram in Fig. 13 vi (= Fig. 10 xx). The only cladogram with which it can be combined to give an informative result is that shown in Fig. 13 vii (= Fig. 12 xxi). However, the same is true for the implied cladograms of Fig. 13 ix (= Fig. 10 xxi) and Fig. 13 x (= Fig. 12 xxii). This means that when a small number of different groups are examined there is some ambiguity about the analyses under the second assumption. However, when all three area cladograms containing the widespread species are combined (Fig. 14) only one fully informative cladogram can be obtained (Fig. 14 xi), derived from the three implied cladograms shown in Figs. 10 xx; 11 xx; 12 xxi. Combining the three cladograms together under assumption one is totally uninformative (Fig. 14 iv–vii).

It must be mentioned that combining the component analyses for the species groups 6 and 7 under assumption one is totally informative (Fig. 14 xii–xiv) and

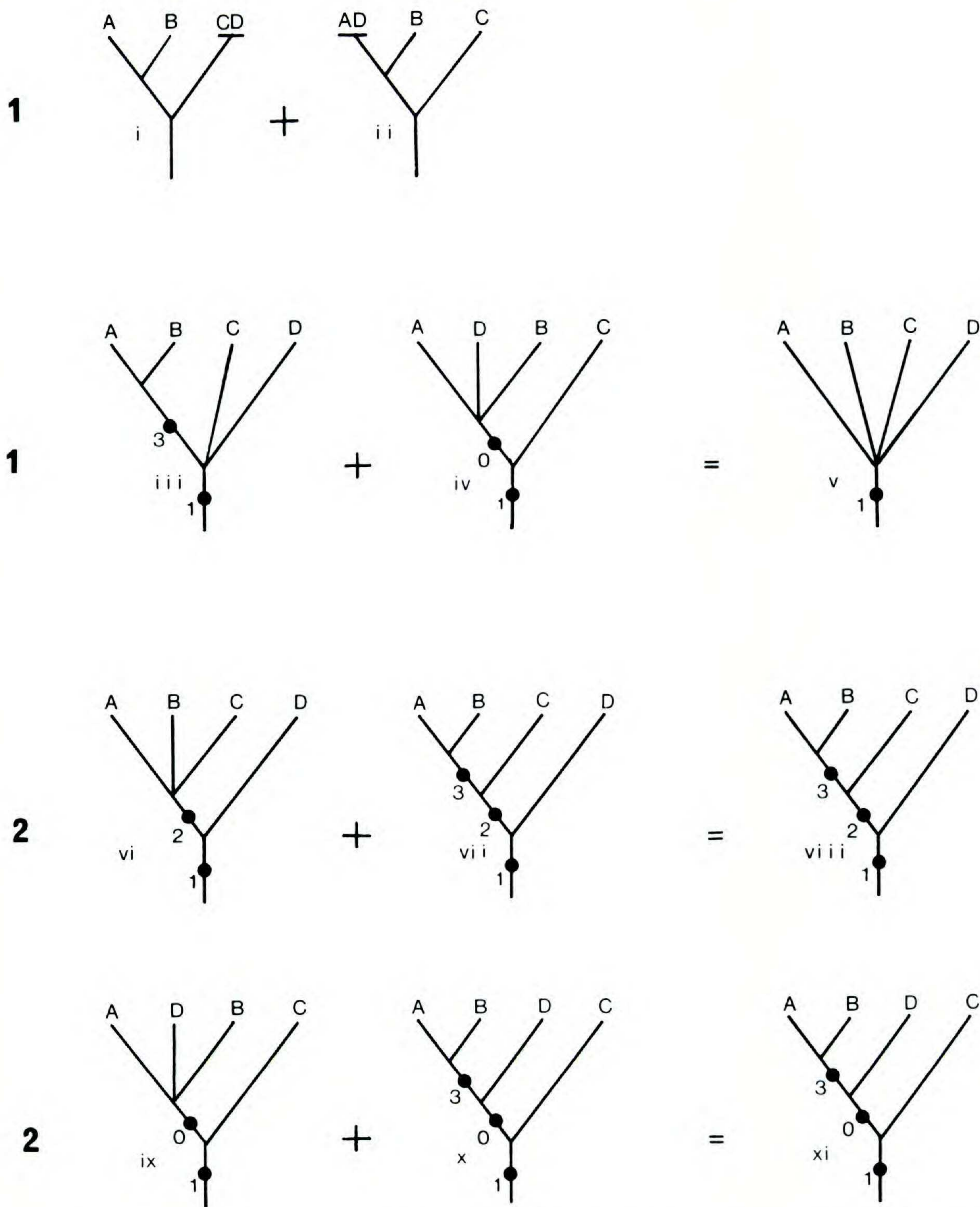


FIGURE 13. Combining components from two species/area cladograms containing widespread taxa to obtain general area cladograms; (i) cladogram from Fig. 10; (ii) cladogram from Fig. 12; (iii–v) combination under assumption 1; (vi–xi) possible combinations under assumption 2. See text for details.

only partially resolved under assumption two (Fig. 14 xv–xvii). This phenomenon occurs only when there is no overlap or conflict in the original data. The overall message from comparing the two different approaches is that assumption two is far less restrictive than assumption one. If there is any information that can be obtained from area cladograms containing ambiguous data, then it is most likely to be extracted by using assumption two.

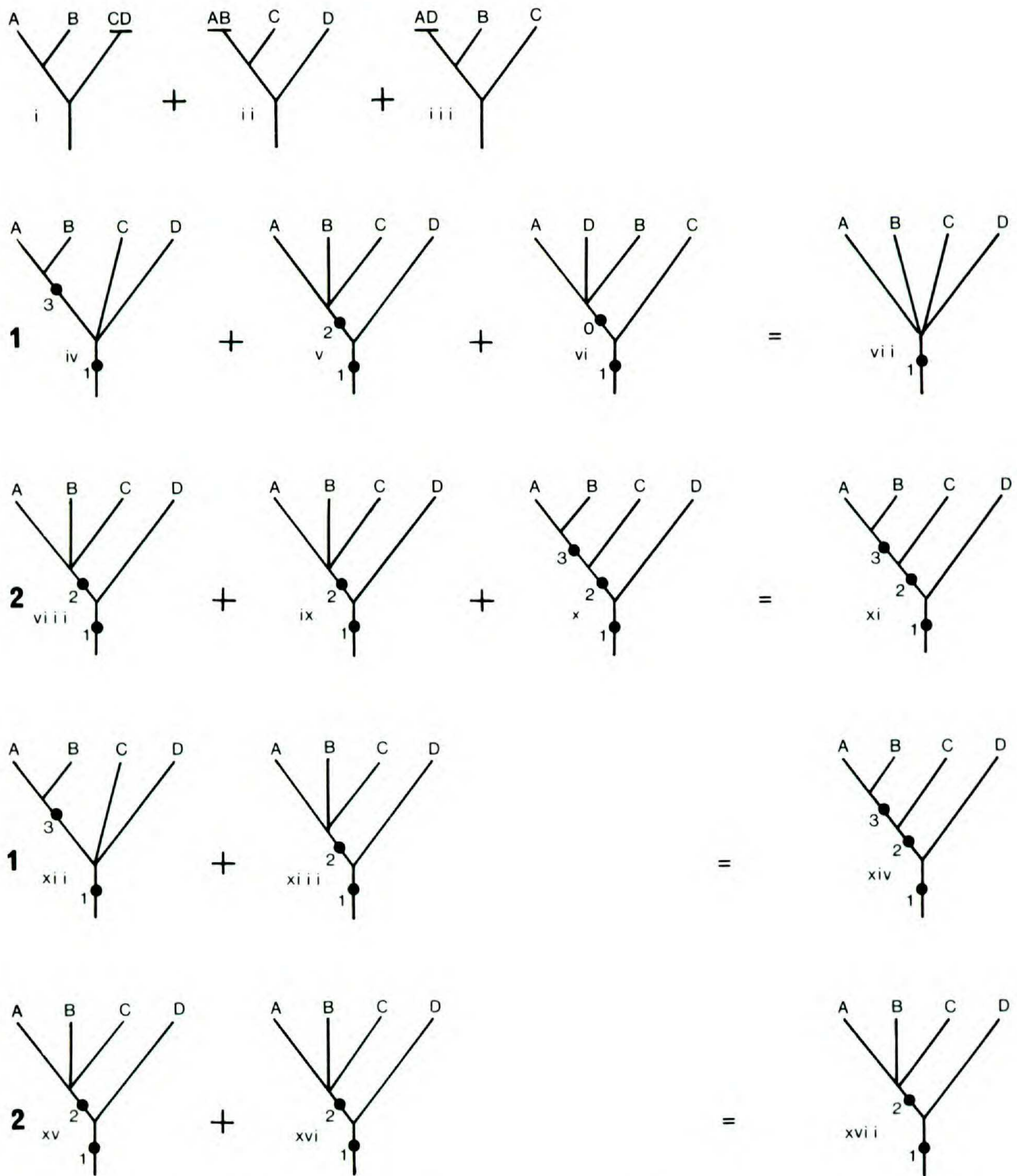


FIGURE 14. Combining components from three and two cladograms containing widespread taxa to obtain general area cladograms; (i–iii) cladograms from Figs. 10, 11, 12; (iv–vii) combinations under assumption 1; (viii–xi) only possible combinations under assumption 2; (xii–xiv) two area cladogram combinations under assumption 1; (xv–xvii) two area cladogram combinations under assumption 2. See text for details.

THE POECILIID FISHES

The two poeciliid fish genera *Heterandria* and *Xiphophorus* are quite widely distributed and each has monophyletic subgroups occurring in the general areas of southern Mexico, south to eastern Honduras, and Nicaragua. The endemics occupy similar, virtually identical areas in Middle America (Fig. 15). The cladograms expressing area relationships based on cladistic analysis are given in Fig.

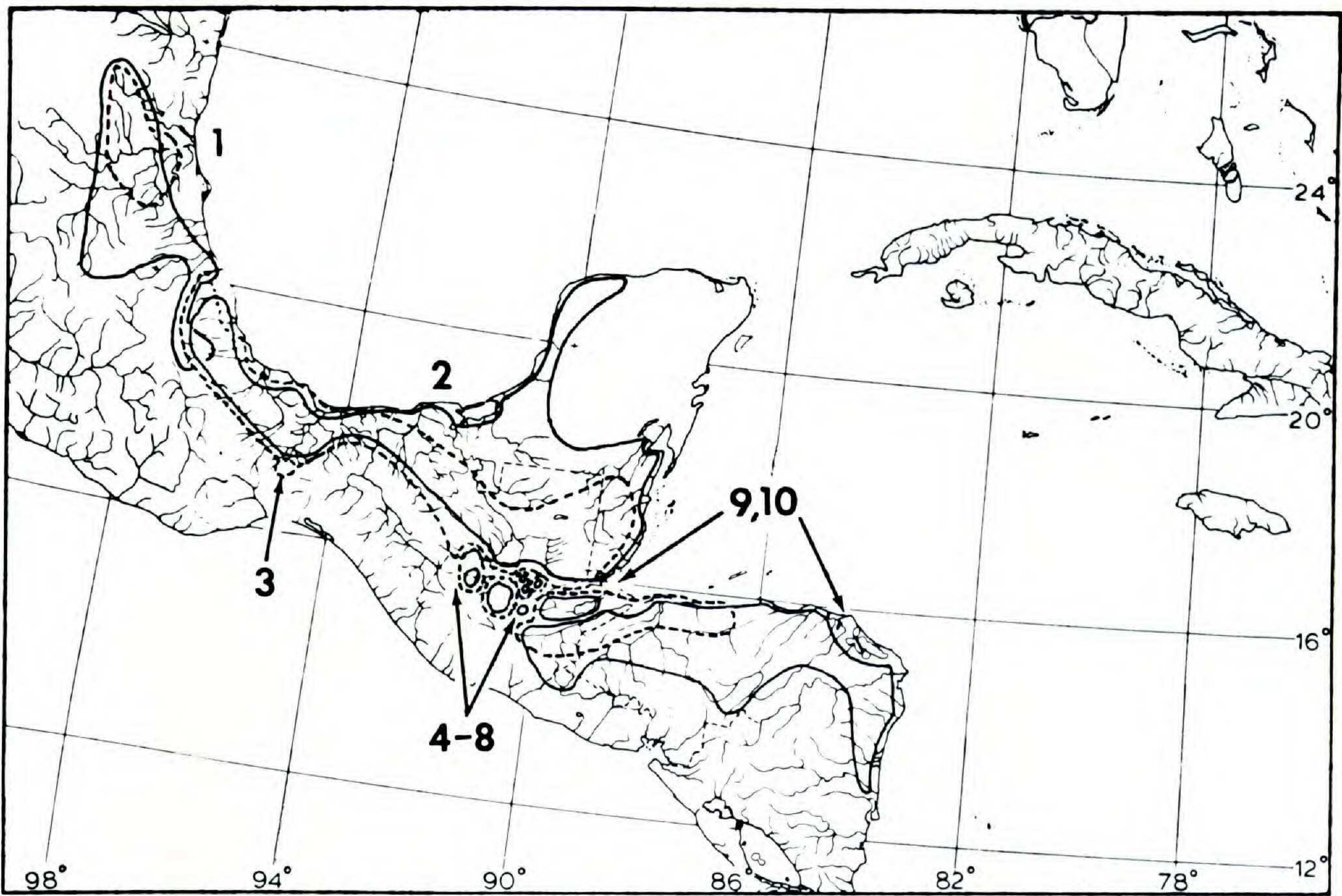


FIGURE 15. Co-occurrences of the middle American species and recognizable populations of *Heterandria* (solid) and the swordtail species of *Xiphophorus* (dashed) within 10 subregions (after Rosen, 1978, fig. 16).

16 (after Rosen, 1978, 1979; Platnick, 1981). The maps and cladograms show that there are eleven identifiable disjunct areas occupied by both species groups. Areas 4 and 5 are occupied by one species in each group and are thus treated as a single area 45. Area 11 was treated by Rosen (1978, 1979) as a hybrid area, but since it is a true disjunct area it is maintained here. Bridging taxa and hybrids have no

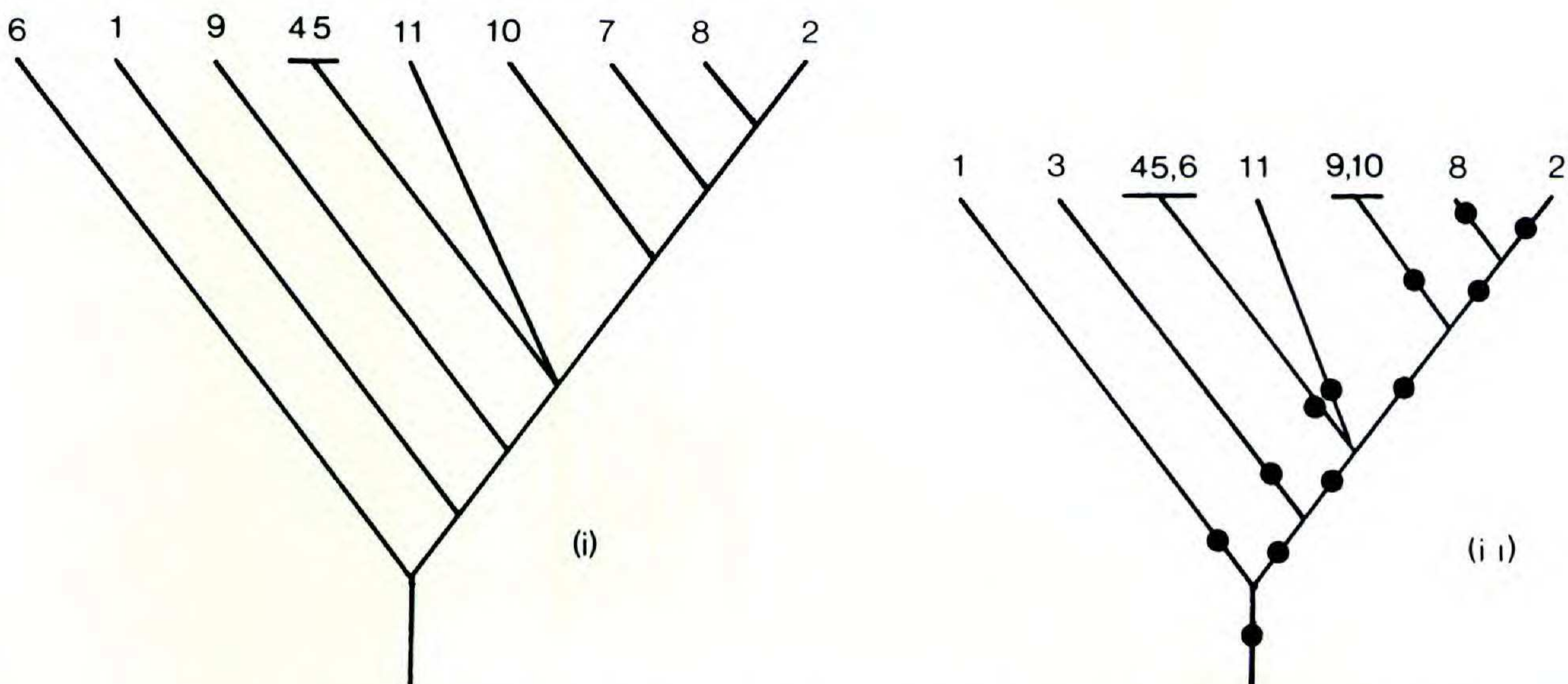


FIGURE 16. Resolved area cladograms for *Heterandria* (i) and *Xiphophorus* (ii) eliminating reticulations (after Platnick, 1981, Figs. 3-6).

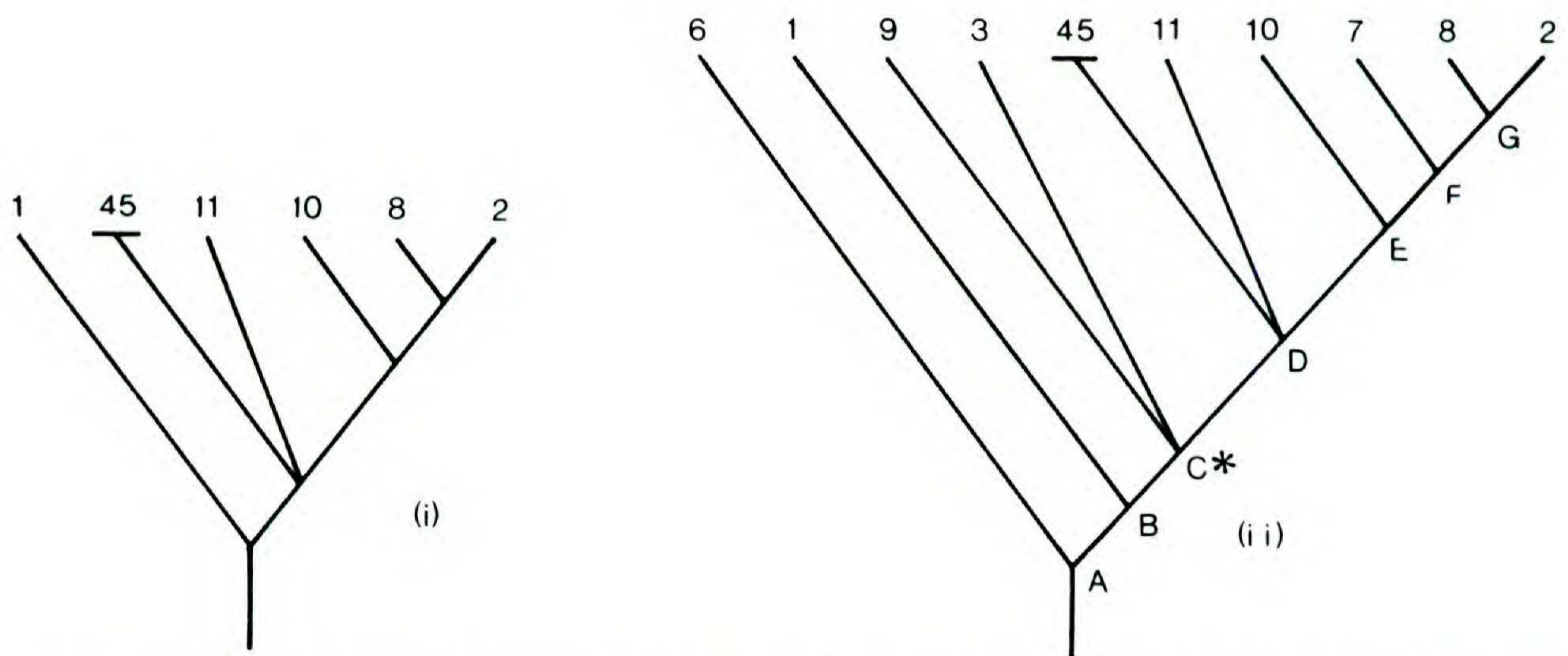


FIGURE 17. (i) Reduced general area cladogram for *Heterandria* and *Xiphophorus* analyzed under assumption 1; (ii) maximally informative cladogram for the areas occupied by *Heterandria* and *Xiphophorus* analyzed under assumption 2 (after Platnick, 1981). For key to letters and asterisk see text. Key to areas Fig. 15.

place in cladistic analysis since they are equivalent to two cladograms added together (see Nelson & Platnick, 1980, 1981). The area 11 containing ambiguous information can be treated as unresolved information and be placed at the ancestral stem.

A comparison of the two cladograms (Fig. 16) shows that *Xiphophorus* is less informative than *Heterandria* because it has two widespread species in areas 45, 6, 9, and 10 and is missing totally from area 7. In *Heterandria* areas 45, 6, 9, and 10 are all occupied by taxa.

As already shown by Platnick (1981) under assumption one whatever is true of a widespread taxon in one part of its range (e.g., *Xiphophorus alvarezii* in area 45) must also be true in another part of its range (area 6). However under as-

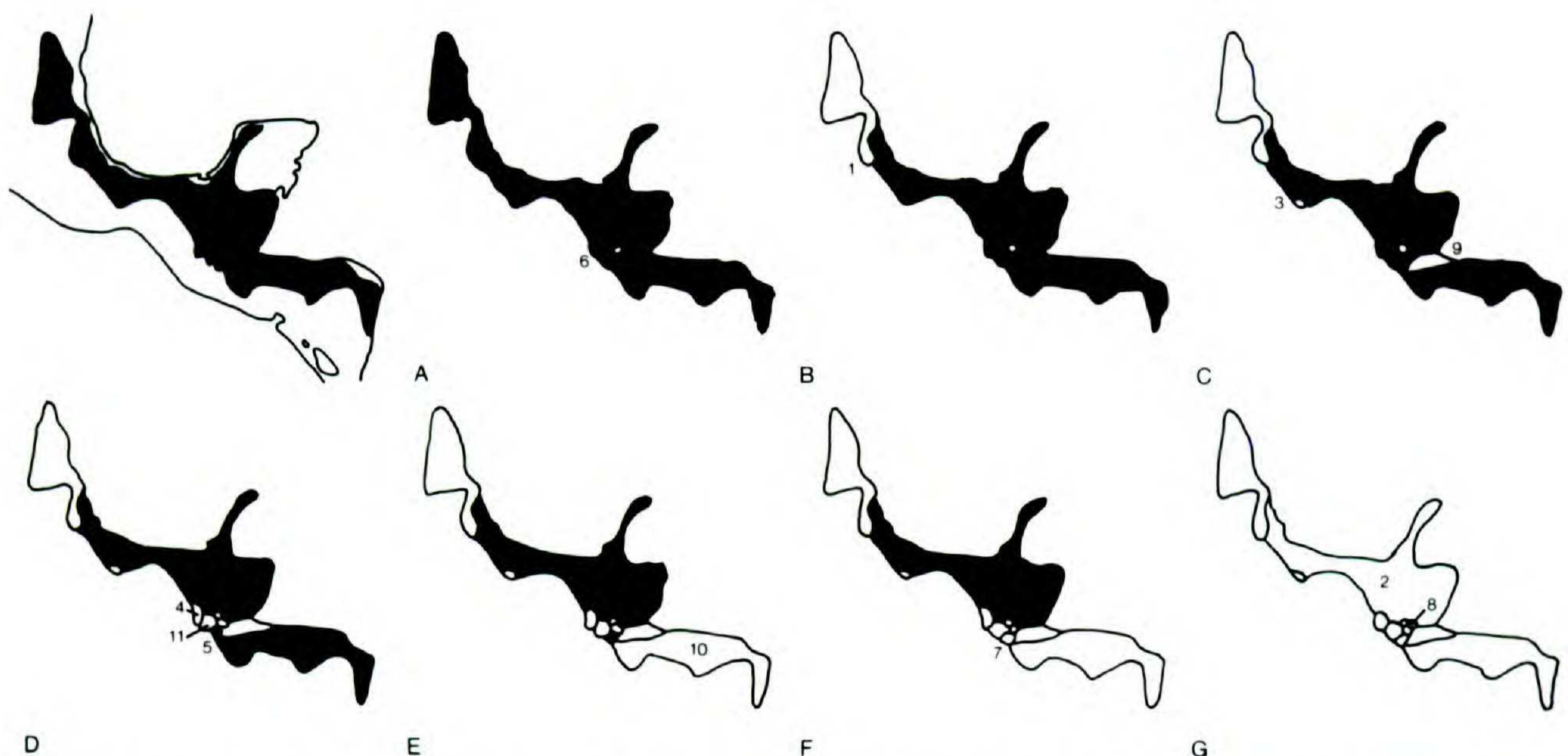


FIGURE 18. Sequence map for 11 areas in Mesoamerica when visualized through assumption 2. Letters refer to Fig. 17 ii.

sumption two whatever is true of a widespread taxon in one part of its range need not also be true of the taxon elsewhere. In other words, the widespread distributions are equivalent to saying that we are ignorant of the reasons for lack of resolution in the cladograms. In terms of distribution, that is equivalent to saying that we do not know whether the patterns are due to dispersal or a failure to speciate in response to a vicariance event. Rosen's original biogeographic method (1978, 1979) compared the two cladograms to one another and identified those parts which were congruent. Incongruent and unique areas were deleted since they were believed to be uninformative. Thus, by removing area 7, unique to *Heterandria*, and areas 3, 6 and 9, common and incongruent to both cladograms, two reduced and equal area cladograms for six areas could be produced. This is a method for obtaining a single statement for each of the congruent areas and Fig. 17 shows the result corrected for area 11. As Platnick (1981) pointed out, the removal of unique and incongruent areas is equivalent to analyzing under the first assumption. If assumption one is adopted then the *Xiphophorus* population of area 9 must be most closely related to the population in area 10, and the information for area 9 incongruent with the information from *Heterandria*. Similarly, the information on area 6 is incongruent for both cladograms.

Platnick (1981) showed that a completely different result can be obtained by applying assumption two. By taking the information on areas 6 and 9 from *Heterandria* as correct, then the incongruent information in the same areas for *Xiphophorus* is either due to dispersal or to a failure to speciate in response to a vicariance event. Rosen's original reasons for applying a version of assumption one was that such evolutionary events reduced the information content of the cladograms. Platnick (1981) noted, however, that if widespread taxa are uninformative they cannot be incongruent at the same time. Absence data can never be incongruent with the data at hand so unique areas should never be deleted. Taken on their own, widespread taxa under assumption two give uninformative components, but, when combined with other cladograms containing widespread taxa, resolved results are possible. Under assumption two the *Xiphophorus* cladogram (Fig. 16 ii) allows the populations in area 9 (or 10, but not both) and area 45 (or 6, but not both) to occur in any of twelve positions shown by black dots. The analysis yields three possible cladograms, all of which are plausible, which can be summarized by a trichotomy as shown by the asterisk in Fig. 17 iic.

THE GEOLOGICAL IMPLICATIONS

Unlike the reduced area cladograms produced by Rosen (1978, 1979) and the cladogram produced here under assumption one, (Fig. 17 i), we have in Fig. 17 ii a cladogram that really does account for all eleven areas of endemism recognized from the two poeciliid fish genera. Taken from a purely vicariant point of view, the historical sequence of events for Mesoamerica that this cladogram implies is illustrated in Fig. 18. If such a pattern is due to changes in earth history, what might the historical factors have been in Mesoamerica and how might these be compared with the biological distributions? So that biotic and historical patterns can be compared we ideally would require that geological information be assembled into cladograms in the same way as biological cladograms. So far this is yet to be achieved. An examination of recent papers by Pinet (1972), Coney (this volume), Muelber-

ger and Ritchie (1975), Howarth (1981), Adams (1981), and Malfait and Dinkelman (1972) still makes it impossible to produce a geological cladogram at the same resolution as given in the most expressive combined, or even reduced, poeciliid fish cladograms (Fig. 17). However, some branch points are borne out by paleogeographic observations. The origin of the Gulf of Honduras occurred in the mid-Mesozoic when rifting along the Cayman trench occurred. The striking slip fault has its landward extension in Guatemala in the Motagua and Polochic faults, which probably represents the northern boundary of the Caribbean Plate. The branching pattern of the cladogram predicts that the events which isolated taxa in areas 6, 1, and 9 (Rio Candelaria, Yalicar, Rio Panuco, and Rio Polochic) preceded those which isolated the Motagua basin (area 10) and coastal Honduras drainage from North Guatemala (areas 7, 8, and 2). The region has been tectonically active ever since the Eocene (Pinet, 1972). Until such time as the geological data can be ordered for a more informative comparison, one can say little except that the observed resolved biological patterns in Mesoamerica have been formed over a period of at least 80 million years (Rosen, 1978).

CONCLUSION

Hopefully, by explaining some principles of cladistic biogeography, I've conveyed the idea that the history of organisms and the history of the earth go together. Cladistics is a general method for discovering the sub-class relations of taxa without recourse to evolutionary narrative. Cladistic biogeography is a natural offshoot from cladistics and is a general method of discovering the sub-class relations of areas by analysis of biological cladograms, again without any recourse to evolutionary narrative. By reconsidering Rosen's studies (1975, 1978, 1979) with Platnick's (1981) reinterpretations, I hope I have underlined the importance of the new Flora Mesoamericana project as an empirical data base for future biogeographical studies on plants from this fascinating part of the Neotropics.

LITERATURE CITED

- ADAMS, C. G. 1981. An outline of Tertiary palaeogeography. In L. R. M. Cocks (editor), *Chance, Change & Challenge*, vol. 1: The Evolving Earth. British Museum (Natural History) & Cambridge University Press.
- BOLICK, M. 1981. A cladistic analysis of *Salmea* DC (Compositae—Heliantheae). Pp. 115–125 in V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics*. Proceedings of the first meeting of the Willi Hennig Society. New York Botanical Garden, New York.
- CROIZAT, L. 1958. *Panbiogeography*. Published by the author, Caracas.
- . (1962) 1964. *Space, Time, Form: The Biological Synthesis*. Published by the author, Caracas.
- DARLINGTON, P. J. 1965. *Biogeography of the Southern End of the World*. Harvard University Press, Cambridge.
- FARRIS, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19: 83–92.
- , A. KLUGE & M. J. ECKHARDT. 1970. A numerical approach to phylogenetic systematics. *Syst. Zool.* 19: 172–189.
- FITCH, W. M. 1977. The phyletic interpretation of macromolecular sequence information: simple methods Pp. 169–204 in M. K. Hecht, P. C. Goody & B. M. Hecht (editors), *Major Patterns in Vertebrate Evolution*. Plenum Press, New York & London.
- & E. MARGOLISH. 1967. Construction of phylogenetic trees. *Science* (Washington, DC) 155: 279–284.
- HENNIG, W. 1965. Phylogenetic systematics. *Ann. Rev. Ent.* 10: 97–116.
- . 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana. Reprint 1979.

- HOLLOWAY, J. D. & N. JARDINE. 1968. Two approaches to zoogeography: a study based on the distributions of butterflies, birds and bats in the Indo-Australian area. *Proc. Linn. Soc. Lond.* 179: 153–188.
- HOWARTH, M. K. 1981. Palaeogeography of the Mesozoic. Pp. 197–220 in L. R. M. Cocks (editor), *Chance, Change & Challenge* vol. 1: The Evolving Earth. British Museum (Natural History) & Cambridge University Press.
- HUMPHRIES, C. J. 1981. Biogeographical methods and the Southern Beeches (Fagaceae: *Nothofagus*). Pp. 177–207 in V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics. Proceedings of the first meeting of the Willi Hennig Society*, New York Botanical Garden, New York.
- JUDD, W. S. 1981. A monograph of *Lyonia* (Ericaceae). *J. Arnold Arbor.* 62: 63–128.
- KLUGE, A. & J. S. FARRIS. 1969. Quantitative phyletics and the evolution of the aurons. *Syst. Zool.* 18: 1–32.
- MALFAIT, B. T. & M. G. DINKELMAN. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. *Geol. Soc. Amer. Bull.* 83: 251–272.
- MOORE, G. W., J. BARNABAS & M. GOODMAN. 1973. A method of constructing maximum parsimony ancestral amino acid sequences on a given network. *J. Theor. Biol.* 38: 459–485.
- MUELBERGER, W. R. & A. W. RITCHIE. 1975. Caribbean-Americas plate boundary in Guatemala and southern Mexico as seen on Skylab IV orbital photography. *Geology* May 1975: 232–235.
- NELSON, G. 1975. Historical biogeography: an alternative formalization. *Syst. Zool.* 23: 555–558.
- & N. I. PLATNICK. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.
- & D. E. ROSEN (editors). 1981. *Vicariance Biogeography: A Critique*. Columbia University Press, New York.
- PARENTI, L. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bull. Am. Mus. Nat. Hist.* 168(4): 341–557.
- PATTERSON, C. 1981. Methods of paleobiogeography. Pp. 446–489 in G. Nelson & D. E. Rosen (editors). *Vicariance Biogeography: A Critique*. Columbia University Press, New York.
- PINET, P. R. 1972. Diapirlike features offshore Honduras: implications regarding tectonic evolution of Cayman trough and Central America. *Geol. Soc. Am. Bull.* 83: 1911–1922.
- PLATNICK, N. I. 1981. Widespread taxa and biogeographic congruence. Pp. 223–227 in V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics: Proceedings of the first meeting of the Willi Hennig Society*. New York Botanical Garden, New York.
- ROSEN, D. E. 1975. A vicariance model of Caribbean biogeography. *Syst. Zool.* 24: 431–464.
- . 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* 27: 159–188.
- . 1979. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bull. Am. Mus. Nat. Hist.* 162: 267–376.
- SANDERS, R. W. 1981. Cladistic analysis of *Agastache* (Lamiaceae). Pp. 95–114 in V. A. Funk & D. R. Brooks (editors). *Advances in Cladistics: Proceedings of the first meeting of the Willi Hennig Society*. New York Botanical Garden, New York.
- WILEY, E. O. 1980. Phylogenetic systematics and vicariance biogeography. *Syst. Bot.* 5(2): 194–220.
- . 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Wiley Interscience.